

A self-consistent approach to paternity and parental effort

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We review the relationship between optimal parental effort and paternity, and emphasize the need for a self-consistent approach. A fundamental consistency condition is what we refer to as the conservation of paternity. Every offspring has exactly one father. If a male has a paternity of less than unity, then another male or other males must have gained the lost paternity. Our approach also emphasizes that paternity emerges as the result of interactions between males and females. From this viewpoint, if paternity changes it is because some aspect of the interaction changes, and the correlation between effort and paternity depends on the aspect that has changed. This has implications for comparative analyses of paternity. The conclusions that are drawn about the correlation between effort and paternity within a population depend on, for example, the types of male in the population and how their abilities are correlated. It is easy to construct models that predict negative correlations between effort and paternity.

Keywords: paternity; parental effort; sex differences in levels of care; consistent models of paternity and parental effort

1. INTRODUCTION

In a wide range of species, males provide some form of care for their offspring (Clutton-Brock 1991). In many of these species, there is evidence that females mate with several males, and that more than one male may be the father of the young in a brood (Birkhead & Møller 1998). This phenomenon has been widely studied in birds. Even when a male and a female form a pair and raise young together, each member of the pair may mate with other individuals. These EPCs may result in EPFs (see Westneat *et al.* (1990); Petrie & Kempenaers (1998) for reviews).

If a female mates with more than one male, a male may not be the father of all the offspring in 'his' brood, i.e. he may not have full paternity. This has implications for the level of parental care that a male should give to the young in the brood. The care that a male gives may reduce his future reproductive success, and so if the young are not likely to be the male's offspring, his best option may be to reduce his level of care in order improve his future prospects. Whether this is indeed optimal will depend on his paternity in future breeding attempts. Maynard Smith (1978) and Grafen (1980) pointed out that if a male's only option is to care for broods in which he has paternity p , then p has no effect on optimal care. Winkler (1987) showed that if a male has paternity p in the current brood and a future reproductive success that is independent of p then optimal male care increases as p increases. In all of these models, a male has a paternity p less than unity, but there was no discussion of who has the missing paternity $1 - p$. Werren *et al.* (1980) were the first to be explicit

about the conservation of paternity, and to build a model that was self-consistent in that all the paternity was accounted for. They considered territorial males and argued that care may increase with paternity because a high value of paternity is associated with limited options for matings outside the territory. It is clear from these examples that the effect of p depends on context, a point made by Westneat & Sherman (1993).

The effect of paternity on care has been the subject of considerable discussion (e.g. Westneat & Sherman 1993; Wright 1998), but the importance of self-consistency has not been systematically explored. Many aspects of paternity only make sense if there are different types of males. Our aim is to develop an approach that includes the possibility of different types of male in a self-consistent way. Paternity emerges because of interactions between males and females. We use our approach to review, clarify and extend our understanding of the relationship between paternity and parental effort. Kempenaers & Sheldon (1997) suggested that the presence of different types of males in a population could produce a negative correlation between effort and paternity. For example, a male in poor condition may have both a low paternity in his current brood and a low future reproductive success. If the effect of the future is strong enough, the male may devote more effort to the current brood than a male with high paternity. We demonstrate how such negative correlations can occur in a self-consistent model.

2. GENERAL ISSUES

So far, we have used 'paternity' in a loose way. We now give a definition of this term. Following Westneat & Sherman (1993), we use the term 'parentage' to refer to the proportion of young in a brood that are actually the off-

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spring of a social parent. A male may not know his parentage but has two sources of information about it. One source is evolutionary—the average proportion fathered in similar circumstances over evolutionary time. In a given reproductive attempt, the male may also have informational cues from his copulatory behaviour and the behaviour of the female and other males. The male's decision about care ought to be based on the expected proportion of young that he has fathered, given all the available information. We refer to this expected proportion as the male's paternity. ('Paternity' is used in other senses; see Schwagmeyer & Mock (1993) for a discussion.) In mathematical terms, parentage may be regarded as a random variable. The evolutionary history specifies the prior distribution for this random variable. In a particular reproductive attempt, cues available to the male allow its distribution to be modified by Bayes' rule to give a posterior distribution. (For a review of the application of Bayes' rule to animal decision-making, see McNamara & Houston (1980).) Paternity is the mean of this posterior distribution. As long as population size is large, which is the case considered in this paper, this mean is the only relevant aspect of the posterior distribution. (If population size is small, other aspects, such as the variance, may be relevant; see Xia (1992).)

By definition, parentage is conserved; if a male has a parentage value of less than unity, then at least one other male must have fathered young in his brood. Consider a group of males that are identical in all respects, including cues as to their parentage. In particular, all have the same paternity p . Within this group, parentage will vary, but paternity will equal the mean parentage in the group. Similarly, the paternity of males from EPCs will reflect their mean parentage in broods of other males. It follows that conservation of parentage implies conservation of paternity.

We are concerned with the effect of paternity on the effort that males devote to care. There are five separate issues:

- (i) Do we expect less parental effort by males than females when males have a paternity of less than unity?

The remaining four issues concern the predicted correlation between male effort and paternity:

- (i) Across successive breeding attempts of the same male
- (ii) Across different males within a population of a species
- (iii) Across populations of the same species
- (iv) Across species.

It is important to keep these issues distinct.

Parental care involves a trade-off between current and future reproductive success (Clutton-Brock 1991). Consider a brood for which the male has paternity p . Let B denote the number of young that survive to independence from this brood. Let V be the residual reproductive value of the male, that is his total reproductive success from all other current and future breeding attempts. Typically, by

devoting effort to the focal brood he increases B but decreases V . The male's optimal level of effort maximizes

$$pB + V \quad (2.1)$$

The conclusions that we reach concerning the effect of paternity are likely to depend on what we assume about the decisions available to an animal, together with the associated trade-offs. For example, Grafen (1980) assumes that a male decides how long to spend caring for his offspring. The trade-off is that an increase in the time spent caring increases the survival of the offspring but wastes time that could have been spent searching for, and mating with, a new female. In the analysis of Werren *et al.* (1980) parental care by a territorial male involves a cost in terms of a reduction of the number of eggs fertilized either on his territory or outside it. The general framework presented by Westneat & Sherman (1993) involves a male allocating effort to caring for the current brood (parental effort) obtaining additional matings (mating effort) and improving the chances of survival (somatic effort), subject to a constraint on total effort. Thus, the usual assumption in models that consider EPCs is that there is a trade-off between care and obtaining additional matings. The reality may be more complex. Although there is evidence in birds that an increase in the opportunity to attract another female results in reduced male parental care, (Smith 1995; Magrath & Elgar 1997), the reduction was observed during incubation. Smith found no effect on the extent to which males fed young. This suggests that in some cases decisions about extra matings may be made before some decisions about care. The details of the decisions available and the trade-offs will depend on the temporal organization of the breeding season, for example whether there are multiple broods and whether breeding is synchronized (Westneat *et al.* 1990). An adequate model might have to involve a series of decisions by the male over the season. There may also be trade-offs associated with mate guarding (Westneat *et al.* 1990). For example guarding one's mate may make it harder to obtain EPCs (Hasselquist & Bensch 1991).

3. A SELF-CONSISTENT APPROACH

In modelling a system, it is often convenient to consider some aspects in isolation from others, i.e. ignore interactions between different components of the system. In some cases, this may give an adequate account of the aspect under consideration. In other cases, ignoring interactions may give a distorted picture. We now describe various interactions that we consider important in an analysis of the relationship between effort and paternity.

(a) *Conservation of paternity*

A fundamental constraint is that in species with two sexes, every offspring produced by sexual reproduction has one father and one mother, so that the total number of offspring fathered by males must equal the total number of offspring produced by females (cf. Fisher 1930). As we shall illustrate, this link between males and females is crucial to a comparison of male and female effort. The constraint is also crucial to the analysis of the correlation between paternity and effort. Because every offspring has exactly one father, if a male has paternity $p < 1$, then

another male, or males, must have gained the lost paternity. To see why this conservation of paternity might be important, suppose that a male has the same paternity on each breeding attempt. Then the residual reproductive value is proportional to p and hence p cancels from expression (2.1) and so has no effect on effort (cf. Maynard Smith 1978; Grafen 1980). However, suppose that all males in the population are the same and that there are equal numbers of mature males and females. Since a male has $p < 1$, other males must have gained EPFs. Thus, since all males are the same, the focal male must have gained EPFs. It follows that the residual reproductive value of the male must contain a contribution from the EPFs as well as the contribution that is proportional to p . This means that p does not cancel out. If, however, not all males are equal, this argument no longer holds for a specific male. In general, we need to consider the consistency of the entire mating system when modelling the effect of paternity on parental care. As the analysis of Werren *et al.* (1980) demonstrates, the conclusions about the effect of paternity on the behaviour of territorial males depend on which males get the missing paternity.

(b) *Paternity emerges*

Is it reasonable to change the value of paternity in a model while everything else remains constant? The paternity p of a male in a given breeding attempt may depend on his behaviour, the behaviour of the female and that of all other males (Westneat *et al.* 1990; Birkhead & Møller 1992; Petrie & Kempenaers 1998). In a fully consistent model of such a system, both effort and paternity would emerge as outputs. From this perspective, if p varies between males within or across populations, this must be because something has changed to change p . As we will demonstrate, what changes in order to change p is crucial in determining the relationship between effort and paternity.

(c) *Different males*

In building a model it is important to specify whether all males in a population are the same and if not how they differ. Males might differ in a variety of ways. For example, they may differ in their ability to provide care or to obtain EPCs. In this case, we say that males differ in type. Even if males are of the same type, they may differ in paternity because they have different cues concerning whether the female has mated with another male. Males may also differ in terms of the time during the season when they breed. This may be because the males differ in type or be the result of chance effects. The conclusions that we draw from a model may depend on how paternity is allocated between different types of males. We have already seen the relevance of this in the discussion of whether p could be cancelled out as a common factor in expression (2.1).

(d) *Remating opportunities*

An important determinant of a male's evolutionarily stable level of care is his chance of finding a new mate if he deserts (Maynard Smith 1977; Grafen & Sibly 1978). The time to remate depends on the care and desertion decisions of other population members. If the focal male is representative of other males in the population, then

remating opportunities must be consistent with his own behaviour. This consistency condition is included in many models (e.g. Maynard Smith (1977) (Model 3); Grafen & Sibly (1978); Yamamura & Tsuji (1993); Balshine-Earn & Earn (1997)). To illustrate the importance of the feedback between behaviour and remating, consider a game between parents in which each decides whether to care or desert. If we assume an arbitrary remating probability for the males we can choose this probability so that males desert and females care. If, however, the remating probability is generated by the behaviour of males and females, then female care may mean that there are no females available for remating. Thus, uniparental care by the female cannot be a solution (see Webb *et al.* 1999). Not only do feedbacks restrict possibilities, they may also extend them. The results of Selten (1980) demonstrate that the above care game can have no mixed ESS for fixed remating probabilities. But as Webb *et al.* (1999) point out, allowing remating probabilities to depend on parental care means that it is possible to have a mixed ESS.

(e) *Male and female effort*

In a consistent game-theoretical approach, the best care decision for the male depends on that of the female and vice versa (Maynard Smith (1977) (Model 3); Grafen & Sibly (1978); Houston & Davies (1985); Yamamura & Tsuji (1993); Sozou & Houston (1994); Balshine-Earn & Earn (1997); Houston *et al.* (1997); McNamara *et al.* (1999); Kokko (1999)). In modelling paternal effort, consideration needs to be given as to whether including this consistency condition is necessary for a qualitative understanding of the relationship between paternity and male effort.

(f) *Life history models*

When we consider self-consistency in the context of models of optimal life histories, there are several principles that emerge in addition to the conservation of paternity.

(i) *Consistency of the future*

The residual reproductive value is not arbitrary; it depends on future options and behaviour (McNamara & Houston 1986; Houston & McNamara 1999).

(ii) *Stable sex ratio and age distribution*

The sex ratio of breeding animals is determined, in part, by mortalities, which are, in turn, determined by the behaviour of males and females. However, the behaviour of males and females is influenced by the sex ratio. Thus, in a self-consistent model the sex ratio is not specified in advance but emerges from the analysis (cf. Gasson 1999). Similarly, the number of males in each age class is determined by male behaviour, but male behaviour depends on paternity, which depends on the number of males in each age class.

(iii) *Stable population size*

Suppose that the population is at a density-dependent equilibrium. Then the evolutionarily stable strategy at this equilibrium should, if used by all population members, generate the original density-dependent equilibrium (Mylius & Diekmann 1995; Houston & McNamara 1999).

Table 1. Summary of general notation.

symbol	interpretation
p	paternity
B	reproductive success of the brood
V	residual reproductive value
T	pre-care time needed to produce young
γ_f	long-term rate of reproductive success (or gain rate) of a female
γ_m	long-term rate of reproductive success (or gain rate) of a male
τ_f	care time of a female
τ_m	care time of a male
λ	rate at which a single male encounters females
π_{pair}	probability that a single female and male pair on encounter
r_{cop}	rate at which a female copulates with her mate
π_{EPC}	probability that a female allows an extra pair male to copulate
s	population sex ratio (male : female)

Our aim is to discuss important general results that emerge when some or all of the above features are included. Many of our conclusions are supported by results from a rate maximization model. We are not advocating that rate maximization is a completely realistic approach (for example, it ignores mortality and age-dependent effects), but many of the qualitative conclusions are probably general and found in other models.

4. THE RATE MAXIMIZATION MODEL

Each member of a population breeds repeatedly over a long time-period, behaving in such a way as to maximize its long-term rate of reproductive success. The basic behavioural cycle is as follows. Single individuals search for a mate. During this search, males also attempt to obtain EPCs. Once a male and female pair, they spend a pre-care time, T , producing young. During this time, the male defends his paternity by repeated copulation with the female, and the female may give other single males EPCs. After the young are produced each pair member decides on the length of time devoted to care. After care each is again single.

All females in the population are identical. Males can be of different types. A type is characterized by three attributes; the ability to attract a mate, the ability to gain EPCs and the ability to defend paternity by copulation. To quantify these attributes each male is assigned three weights; π_{pair} , π_{EPC} and r_{cop} . A single male encounters females in the population as a Poisson process of given rate λ . We assume, for simplicity, that females that are encountered are drawn at random from the population, irrespective of whether they are single or mated. If an encountered female is single then she pairs with the male with a probability of π_{pair} . A mated female copulates with her mate during the pre-care phase at a rate equal to his copulation weight, r_{cop} . Each single male encountered during this phase copulates with the female with a probability equal to his EPC weight, π_{EPC} . (The notation is summarized in table 1.)

The above parameters, together with the numbers of males of each type, are all inputs to the model. Paternity

emerges as follows. The paternity of a male in his brood is the expected proportion of all copulations of his mate that are with him. Similarly, the paternity of an extra-pair male that copulates with the female is the expected proportion of all copulations that are with him. The paternity of a male of a given type is the same in each brood; in particular, there is no variation that might arise because males have different cues in different reproductive attempts.

In this model, an individual only makes a decision about the length of time to devote to care. If the female cares for time τ_f and the male cares for time τ_m , the success of the brood is $B(\tau_f, \tau_m)$. Females and males are equally good at providing care, so that B is a symmetrical function of τ_f and τ_m . B increases with both τ_f and τ_m but at a decreasing rate. Furthermore, the benefit to the brood from an increase in the effort of one parent decreases as the effort of the other parent increases (details in Appendix A).

Suppose that the female's long-term rate of reproductive success is γ_f , the male has paternity p and his long-term rate of reproductive success is γ_m . Time spent caring for the current brood is costly in that it reduces the time that can be devoted to obtaining reproductive success in the future. If the female spends time τ_f caring she could have achieved a future reproductive success $\gamma_f \tau_f$ in this time. Thus her net gain in reproductive success is

$$B - \gamma_f \times \tau_f \quad (4.1)$$

(McNamara 1982). Similarly, the male's net gain in reproductive success is

$$pB - \gamma_m \times \tau_m. \quad (4.2)$$

In deciding their care times, the female and male members of a pair play a game against one another in which the care time of each is the best given that of the other (cf. Maynard Smith 1977; Grafen & Sibly 1978). These care times have the property that the female's care time maximizes expression (4.1) and the male's care time maximizes expression (4.2). Note that maximization of expression (4.2) is also equivalent to maximization of

$$B - (\gamma_m/p) \times \tau_m. \quad (4.3)$$

As different types of male have different values of γ_m and p , male care time will depend on male type. All females have the same γ_f , but since a female's optimal care time depends on that of her partner, the care time of a female depends on her partner's type.

Comparing expressions (4.1) and (4.3) we can interpret both the male and female as gaining the same benefit, B , from the game, but differing in their cost per unit time. If the female's cost γ_f is less than the male's cost γ_m/p then the female cares for a longer time than the male. Similar reasoning applies to a comparison of male efforts across a population: male care time is negatively correlated with γ_m/p .

What we have described is the solution to the game for given γ_f , γ_m and p . However, these quantities are not specified in advance. They emerge (together with the care times) from a self-consistent account of all the interdependencies in the model. These interdependencies can be summarized as follows. (i) Remating times for males depend on the number of single females. Remating times for females depend on the number of single males of each

type. (ii) Paternities depend on the number of single males of each type. EPFs depend on the number of single males of each type and the number of single females. (iii) The number of single females and numbers of single males of each type depend on the care and remating times of all population members. (iv) Care times depend on paternities and long-term rates of reproduction. (v) The long-term rate of reproduction of a male depends on his remating time, paternity, EPFs, his care time and female care time with a mate of his type. (vi) The long-term rate of reproduction of a female depends on her remating time, the likelihood her mate is of each type and the care times of her and her mate with each type of mate.

We now discuss the five issues regarding paternity and male effort as listed in § 2.

5. ISSUE 1: COMPARING MALE AND FEMALE EFFORTS

In comparing male and female efforts, the fundamental constraint is that every individual has exactly one father and one mother. The implications of this constraint are most clear when all males are the same (and all females are the same). We first analyse this case and then explore the consequences of allowing males to differ.

(a) All males the same

Consider the rate maximization model with all males in the population having the same abilities. In this model, they then have the same constant paternity as one another at every breeding attempt. Females get all their reproductive success through their own reproductive bouts. Males get reproductive success partly through the young of females that they pair with and partly through EPFs. Regardless of how male success is partitioned we must nevertheless have

$$\gamma_m \times (\text{male number}) = \gamma_f \times (\text{female number}), \quad (5.1)$$

since every offspring has one mother and one father (Maynard Smith 1977; Grafen & Sibly 1978). From expression (4.1) the cost of care per unit time to the female is γ_f . By expression (4.3) the equivalent cost to the male is γ_m/p . Thus the male should put in less effort if $\gamma_m/p > \gamma_f$. By the balance equation, i.e. equation (5.1), the male should put in less effort if

$$ps < 1 \quad (5.2)$$

where $s = (\text{male number})/(\text{female number})$ is the sex ratio in the population.

When there are equal numbers of males and females, criterion (5.2) implies that males should put in less effort than females if $p < 1$. We noted earlier that even if males have the same paternity each time, this does not mean that we can cancel out p and deduce that paternity has no effect. Our conclusions here agree with those of Queller (1997) and arise for similar reasons.

It is possible to apply similar ideas to an analysis of male versus female effort in a life history model. However, as the following example shows, the demands of consistency can introduce an important complication.

Suppose that females breed once a year. At the beginning of a breeding season the sex ratio is equal. Males and

females pair up. There then follows a period during which all fertilizations take place. As a result, all males have the same paternity $p < 1$ and the EPFs are divided equally between them. The male and female members of a pair then decide on their effort. Increased effort by a parent increases the survival probability of the current young, but decreases the parent's condition at the end of the breeding season, and hence decreases the probability that the parent survives until the next breeding season. In the effort game between the parents, males and females have symmetrical roles. The cost of care is also the same for both sexes. In particular, if each sex puts in the same effort, then each has the same chance of survival. Thus, the only asymmetry between a male and a female is that the male has reduced paternity. The female's effort should maximize

$$B + V_f \quad (5.3)$$

and the male's effort should maximize

$$pB + V_m, \quad (5.4)$$

where V_f and V_m are the reproductive values of the male and female, respectively, at the end of the breeding season. Because each future offspring has exactly one mother and one father, at the end of the breeding season the sum of the reproductive values of all males equals the sum of the reproductive values of all females (this sum includes contributions from newborn offspring alive at this time) (Fisher 1930). Therefore, if equal numbers of male and female offspring survive until the end of the breeding season, and, as we have assumed, the adult sex ratio is $s = 1$, then it must be the case that $V_f = V_m$. It then follows from expressions (5.3) and (5.4) that the male should put in less effort than the female.

The above argument has mirrored the argument in the rate maximization model, but there is a problem of consistency. If males expend less effort than females, then more males than females survive to breed again in future seasons. Thus, the population sex ratio cannot be unity, and is instead male biased. This in turn implies that $V_f > V_m$, which contradicts our earlier argument.

A self-consistent model would need to incorporate the effect of behaviour on the sex ratio and the effect of the sex ratio on reproductive value via its effect on mating opportunities. It seems probable that such a model would still predict less effort by males than by females, even if the effects are not as strong as predicted when the sex ratio is artificially constrained to be unity.

We note that criterion (5.2) may not be met when $p < 1$ and $s > 1$. This means that in a male-biased population, males may put in more effort than females even though their paternity is less than unity.

(b) Males differ

When males differ, there will be a variation in the parental effort of both males and their female partners across mated pairs in the population. A comparison of male and female efforts must, therefore, now be based on some suitable measure of average effort. We illustrate this in the context of the rate maximization model with equal numbers of males and females ($s = 1$). Suppose that males are classified as discrete types. Let a proportion $\rho(i)$ of these males be of type i . Recall that the model specifies, for each

type of male, the probability that a searching female pairs with the male on encountering him, his copulation rate with his mate and his ability to get EPCs when single. The gain rate of the female, γ_b is then a model output. Other outputs include, for each i : the gain rate of a male of type i , $\gamma_m(i)$; the care times $\tau_m(i)$ and $\tau_f(i)$ of the male and female respectively when the male is type i ; and the proportion of a female's matings that are with a male of type i , $\alpha(i)$. Let

$$\bar{\gamma}_m = \sum_i \rho(i) \gamma_m(i), \quad (5.5)$$

be the average male gain rate. Then when $s = 1$ the analogue of equation (5.1) is

$$\bar{\gamma}_m = \gamma_f. \quad (5.6)$$

In consequence, some males achieve higher gain rates than females and some lower.

We first compare male and female care times when all males have a paternity of unity. In this restricted case males can only differ in the time taken to pair with a female. Those males that take longer achieve a lower gain rate than females and care for a longer time than their partner. Those males that take shorter times care for less time than their mates. Note that in this case, females prefer those males that contribute less parental effort. For this choice to make evolutionary sense, females must obtain some benefit, other than care, that we have not explicitly modelled.

To compare average times let

$$\bar{\tau}_m = \sum_i \rho(i) \tau_m(i) \text{ and } \bar{\tau}_f = \sum_i \rho(i) \tau_f(i), \quad (5.7)$$

be averages across males in the population. Suppose that the success of the brood, B , is a quadratic function of the male and female care times, as in Appendix A. Appendix B demonstrated that the constraint given by equation (5.6) implies that $\bar{\tau}_m = \bar{\tau}_f$ so that if an average across male population members is considered then the mean care times are equal.

Instead of using a male average, we could also utilize an average across the broods produced by a female. Let

$$\tau_m^\# = \sum_i \alpha(i) \tau_m(i) \text{ and } \tau_f^\# = \sum_i \alpha(i) \tau_f(i). \quad (5.8)$$

Compared to $\bar{\tau}_m$ and $\bar{\tau}_f$, these averages emphasize males that are chosen preferentially by the female. These males have a higher gain rate than less preferred males. Their care times are thus shorter and the care times of their female partners are longer. It follows that

$$\tau_m^\# < \bar{\tau}_m \text{ and } \tau_f^\# > \bar{\tau}_f. \quad (5.9)$$

Thus when $\bar{\tau}_m = \bar{\tau}_f$ we have $\tau_m^\# < \bar{\tau}_m = \bar{\tau}_f < \tau_f^\#$.

Suppose that some males have a paternity of less than unity. When the success of the brood, B , is a quadratic function of the male and female care times, as in Appendix A, then $\bar{\tau}_m < \bar{\tau}_f$ (see Appendix B). However, inequalities (5.9) need not hold. Figure 1 illustrates a case in which there are two types of males. Females prefer to mate with type 1 males, but these males obtain no EPCs. Despite the fact that they take longer to pair, type 2 males gain sufficient EPFs to make their gain rate higher than type 1

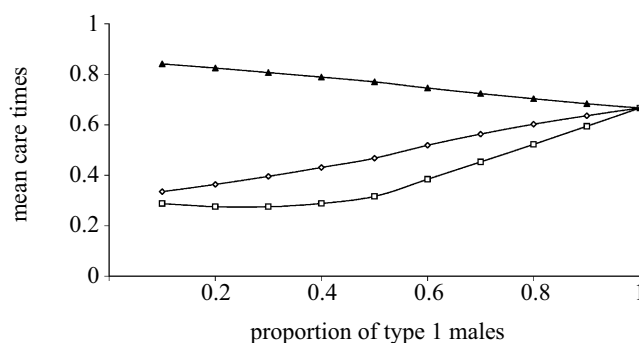


Figure 1. Comparison of male and female care. Rate maximization model with two types of males. The figure shows mean care times as the proportion of type 1 males varies. Mean over the broods produced by a female is given by equation (5.8). Mean over males is given by equation (5.7). $T = 1.5$, $s = 1$, $\lambda = 0.75$. Type 1 males: $\pi_{\text{pair}} = 1$, $\pi_{\text{EPC}} = 0$ and $r_{\text{cop}} = 1$. Type 2 males: $\pi_{\text{pair}} = 0.2$, $\pi_{\text{EPC}} = 10$ and $r_{\text{cop}} = 1$. Filled triangles: female—mean over broods; open diamonds: male—mean over broods; open squares: male—mean over males.

males. Thus type 2 males care less than type 1 males. Since the females prefer to mate with the males that care more, both inequalities (5.9) are reversed. Note that in this example, female choice is consistent with the parental effort of the male.

6. ISSUE 2: CORRELATIONS ACROSS SUCCESSIVE BREEDING ATTEMPTS

(a) *Random versus systematic variation*

We have taken a male's paternity to be the expected proportion of offspring sired by the male conditional on any information available to him. Cues that provide the male with information may vary both between males in the population and between successive attempts of the same male. In some circumstances, it is reasonable to assume that the paternity of a male in a particular reproductive attempt is not correlated with his paternity in subsequent attempts. For example, consider a male that has many reproductive encounters during his life. In some of these encounters he will have observed his partner giving EPCs to other males, and this will lower his paternity (i.e. his estimate of parentage) in these encounters. If future paternity is independent of current cues, then the male should expend less effort in the current reproductive effort if paternity is low, i.e. if he has observed the female giving EPCs.

The above argument amounts to varying p in expression (2.1) while holding V fixed. It is well known that optimal male effort is positively correlated with paternity in this instance (Winkler 1987; Westneat & Sherman 1993). A different scenario might be that males in a population differ in their attractiveness. The more attractive a male is, the fewer EPCs his partner gives to other males. Now a male that observes his partner giving an EPC to another male gains information about his own attractiveness and hence his paternity in future broods. A decrease in p in the current brood brought about by the male observing an EPC of his partner will now be accompanied by a decrease in V . It is still probably true that a decrease in p

will result in a decrease in effort, but the effect is unlikely to be as strong.

The two contrasting scenarios are relevant to an understanding of the effect of an experimental manipulation of paternity. The effect of such a manipulation will depend on how the male views what has happened. If a reduction in paternity is viewed as just bad luck in this attempt and is not seen as an indication of what will happen in future encounters, then the manipulation has effectively reduced p in expression (2.1) while holding V fixed. Conversely, if the reduction in p is perceived as an indication of what will happen in future encounters then both p and V are effectively reduced. For an analogous discussion in the context of predation, see McNamara & Houston (1994).

(b) Effects of age

Within a population, both effort and paternity may vary with age. We explore this relationship in a life history context, for simplicity assuming that each male looks after, at most, one brood per year. As in the section on male versus female effort, a parental male's paternity and the EPFs that he achieves are determined before the period of care. The cost of care is thus a reduction in the condition of the male at the end of the breeding season, and hence a reduced probability that he will survive until the next breeding season. A male with paternity p maximizes expression (2.1), where V is the male's reproductive value at the end of the breeding season. If we follow a male through his life history, the crucial variable is p/V , and effort in any reproductive encounter will be an increasing function of this quantity. The relationship between paternity, reproductive value and age depends on how the paternity of offspring is shared out between the males within the population. We illustrate this in two contexts.

(i) Parental males obtain no EPFs and an age-dependent pattern of paternity is imposed

Males of one type (parental males) gets no EPFs, males of the other type (alternative males, parasitic males or sneakers, i.e. males with an alternative life history—see Charnov (1993); Taborsky (1994); Gross (1996); Henson & Warner (1997)) obtain the missing paternity. We consider this scenario, assuming that the age-dependent paternity of parental males is a given function that arises from the activity of the non-parental males. (We note that a complete account would explain the existence and frequency of the alternative males.) A parental male faces a trade-off between the effort that it devotes to care of the current young and the probability that it survives to breed again next year. If life-history trade-offs do not depend on age, and paternity does not change with age then the effort of a parental male will not change with age. Furthermore, reproductive value is proportional to future paternity, p . Thus p can be taken out as common factor in expression (2.1) and the effort of a parental male is independent of p . If life-history trade-offs do not depend on age but p changes with age then, in general, V depends on future paternity and future effort. To incorporate the future in a self-consistent way over a lifetime, it is natural to work backwards over the lifetime using dynamic programming (Houston & McNamara 1999; Clark & Mangel 2000) to find the optimal effort and the associated reproductive value. It is still true that effort is an increasing function of

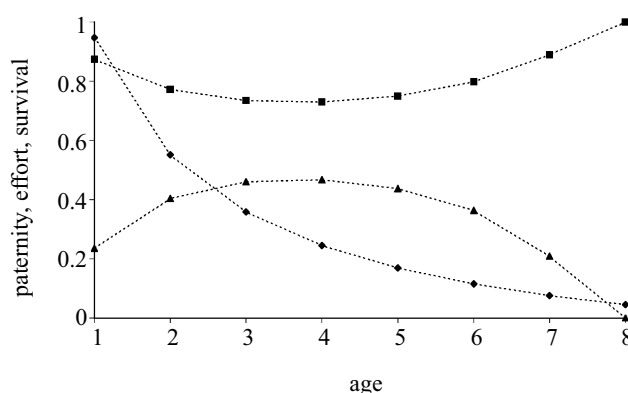


Figure 2. The effort that maximizes lifetime reproductive success. Paternity is taken to decrease with age in the manner shown in the figure. At each age, the male chooses an effort u , where $0 \leq u \leq 1$. The gain from the current brood is proportional to u , and the probability that the male survives to the next year is $0.95(1 - u^2)$. The figure shows the optimal effort together with the resulting annual survival. Filled squares: effort; filled triangles: survival; filled diamonds: paternity.

p/V , but this does not mean that paternity and parental effort are correlated along a life-history trajectory. As Westneat & Sherman (1993) point out, a male may have the same value of paternity at two different ages and yet its optimal level of effort may differ because V differs. Gasson (1999) shows that effort is constant with age if, and only if, $p(t+1)/p(t)$ is constant, in other words paternity depends geometrically on age (not linearly as suggested by Westneat & Sherman (1993)). The level of effort predicted decreases as the value of this constant increases. When $p(t+1)/p(t)$ is not constant, effort may be a non-monotonic function of paternity. An example of this is illustrated in figure 2. In this example, paternity is monotone decreasing over the lifetime of the male, but effort first decreases and then increases.

In the general case involving age-dependent trade-offs, many effects may be possible. In particular, a higher paternity in a male's first year does not mean that his effort in this year should be higher than in subsequent years. For example, an increase in effort may have a greater survival cost in a young male than in an older male. This may favour a lower effort in a young male even though paternity is high.

(ii) All males have the same life history

If it is assumed that the only difference between males in a given season is age, age can determine the ability to guard a female and the ability to get EPCs. Paternity and EPFs emerge from the mixture of male ages in the population. V now depends on the paternity and EPFs in the future. A proper analysis has to give a time-consistent account. A crucial question in this case is how EPFs depend on age.

7. ISSUE 3: CORRELATIONS WITHIN A POPULATION

We now focus on a particular breeding attempt of a population and investigate how the effort of males within

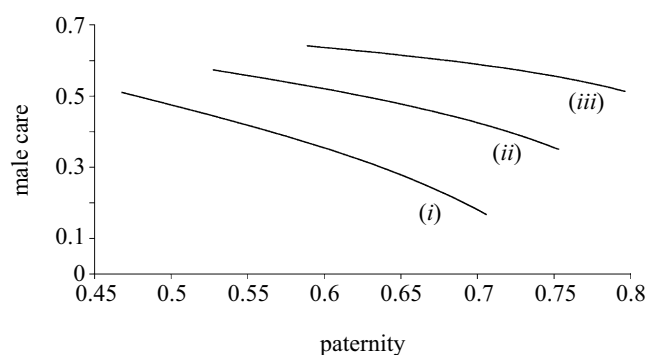


Figure 3. Males differ in quality. High quality males are better able both to defend their paternity and to gain EPFs than low quality males. When each type of male adopts its best effort, a negative correlation between paternity and male care results. Rate maximization model with $s = 1$, $\lambda = 2$. (i) $T = 0.5$, (ii) $T = 1$, (iii) $T = 2$.

the population depends on their paternity. There is an obvious link with the previous case in that the current case can be regarded as a snapshot of males at different ages or stages of their life history. For example, if all males in the population are *a priori* the same, and vary only in the cues that they have about p in the current brood, then there would be a positive correlation between paternity and effort. In general, we again need to know who gets paternity and EPFs. We use the rate maximization model to illustrate some of the effects that are possible.

Within the context of rate maximization, the key to the male's behaviour is the dependence of γ_m/p on p . Paternity depends on a male's copulation weight. γ_m depends on π_{pair} , paternity, and the rate at which the male can get EPFs. These dependencies enable us to vary γ_m and p across males. For example, assume that each type of male has a different π_{pair} , but that all males have the same π_{EPC} and r_{cop} . Now individuals differ in γ_m but all males have the same paternity. Effort decreases with increasing γ_m . Note that paternity is not the driving factor: effort varies across males even though paternity is constant. If instead all males have the same π_{EPC} and π_{pair} but r_{cop} varies across males, then males with high r_{cop} have high paternity. The increase in paternity increases γ_m , but not sufficiently to increase γ_m/p . As a result, there is a positive correlation between effort and paternity across males. Now assume that males differ in more than one ability. The sort of correlation that we get depends on how r_{cop} is correlated with π_{pair} , or π_{EPC} with π_{pair} . Existing data do not tell us much. In birds, males defend their paternity by guarding a female or by frequent copulation (Birkhead & Møller 1992). It is clear that males differ in their ability to obtain EPCs and EPFs, (Kempnaers *et al.* 1995; Møller & Tegelstrom 1997; Yezerinac & Weatherhead 1997; Otter *et al.* 1998) but it is not clear exactly what trade-offs are involved. Many studies involve natural variation, but as Kempnaers & Sheldon (1997) point out, there are limits to what we can deduce from such variation. In some cases a male that is good in some ways will be poor in other ways. In other cases there may be a positive correlation between abilities (some males are generally good). An illustration of what is possible in this case is shown in figure 3. We assume that males can be of differ-

ent qualities where quality affects the ability to defend paternity and obtain EPCs. We thus assume that both π_{EPC} and r_{cop} increase as quality increases, but also assume that $\pi_{\text{EPC}}/r_{\text{cop}}$ increases as quality increases. Females are non-selective about the male that they pair with, so that $\pi_{\text{pair}} = 1$ for all males. Given these assumptions, high quality males have higher paternity because of their ability to defend their paternity. They also gain more EPFs than low quality males. As a result, as quality increases, γ_m increases more rapidly than p and the ratio γ_m/p increases. When each type of male adopts his best effort, a negative correlation between p and τ_m results.

8. ISSUE 4: CORRELATIONS ACROSS POPULATIONS WITHIN A SPECIES

We now compare a series of populations of the same species and investigate the correlation of effort with paternity using the rate maximization model.

(a) Sex ratio

Consider different populations of the same species, with populations differing only in the sex ratio, s . We look at the effect of changing s while holding total population size (number of males plus number of females) constant. We assume that the factor that results in a change in s does not change any of the other parameters in the rate maximization model. The effect of increasing s on male effort can be understood in terms of the way that s influences three factors: (i) the time to find a mate, (ii) paternity, and (iii) partner's effort. As s increases, females take less time to find a mate, there are thus less single females and hence male search time will increase. This will decrease γ_m (see figure 4a) and hence tend to increase male effort. Thus, even without any EPCs ($p = 1$) we can expect male effort to increase as s increases (cf. Grafen & Sibly 1978). If there is a possibility of gaining EPCs then we can expect paternity to decrease as s increases (figure 4a), and this will tend to decrease male effort. The above two counter-acting pressures can result in γ_m/p first increasing and then decreasing (see figure 4a). Thus as s increases, effort initially decreases because of the decrease in paternity and then increases because of the decrease in γ_m (see figure 4b). A further effect, which is weak in our example, is that as s increases, the time for the female to pair will decrease. This exerts a pressure on the female to decrease τ_f (see figure 4b). The result is a pressure on the male to increase τ_m . Combining the results from figure 4a and b, we obtain a non-monotonic relationship between male care and paternity. This is illustrated in figure 5, together with two other examples.

In the above analysis we assumed that populations might differ only in s . It is probable, however, that an environmental factor that influences s will have other effects. To investigate the relationship between sex ratio, care and effort across populations, it would therefore be necessary to construct a self-consistent life history model in which all three quantities emerge as outputs.

(b) The activity of alternative males

Populations might differ in terms of the paternity that is obtained by alternative males. To investigate this we assume that the sex ratio is unity and that there are two

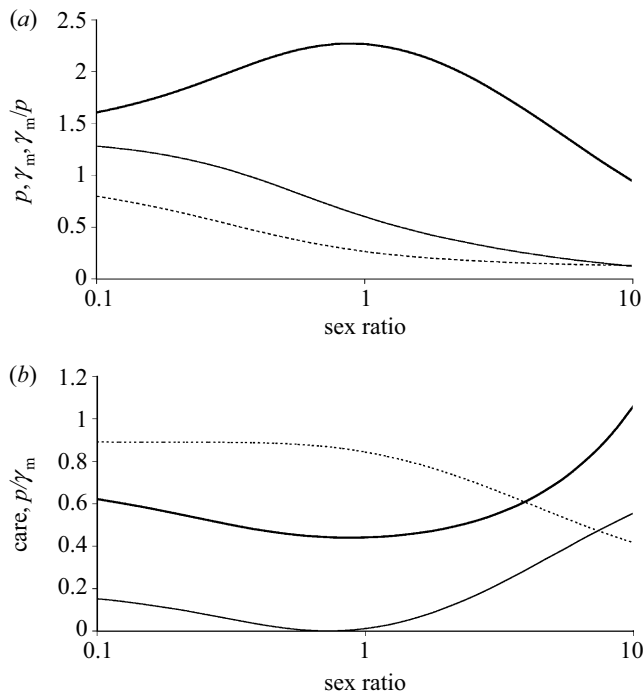


Figure 4. Effect of variation in sex ratio, s , across populations. Rate maximization model with $T = 1$, $\lambda = 1$, $\pi_{\text{EPC}} = 4$, $r_{\text{cop}} = 1$, $\pi_{\text{pair}} = 1$. Interaction parameter $\beta = 0.5$ (see Appendix A for definition). (a) Paternity p (dotted line) male gain rate γ_m (solid line); and the ratio, γ_m/p (bold line). (b) Male (solid line) and female (dotted line) care times together with the ratio p/γ_m (bold line).

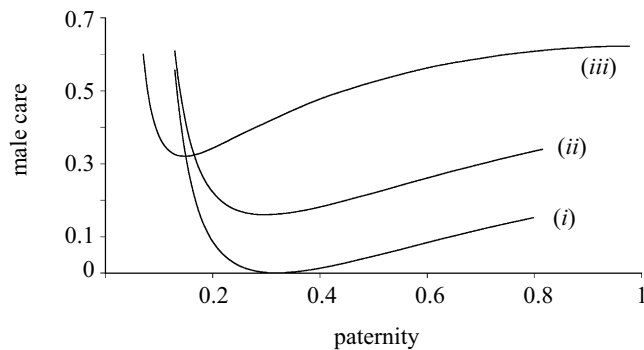


Figure 5. Effort versus paternity when sex ratio, s , varies across populations. Rate maximization model with the following parameters: (i) same as shown in figure 4; (ii) same as (i) except that β takes its standard value of 0.2; (iii) $\lambda = 8$, $T = 4$, $\pi_{\text{pair}} = 1$, $\pi_{\text{EPC}} = r_{\text{cop}} = 1$.

types of male, territorial males and sneakers. The female strongly prefers to mate with the territorial males (this preference is found in several species of fishes, for example, Taborsky (1994)). Sneakers get all the EPCs (cf. Werren *et al.* 1980). The correlation between effort and paternity across populations depends on what we vary in order to vary paternity.

- (i) *Ability of sneakers to get EPCs.* Across populations sneakers differ in terms of their ability to get EPCs.

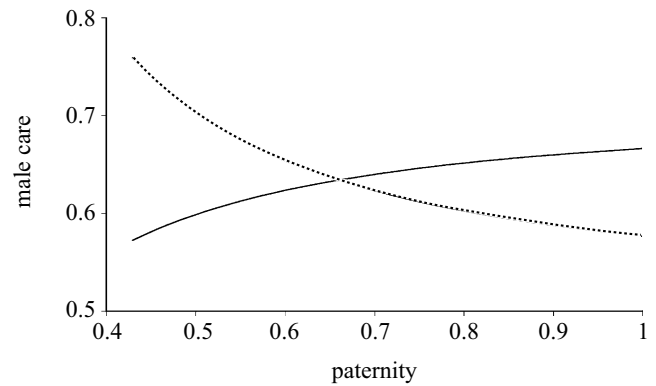


Figure 6. The effect of the proportion of males that are sneakers on the relationship between paternity and male care. Rate maximization model with $T = 1.5$, $s = 1$, $\lambda = 0.75$. Territorial males (solid line): $\pi_{\text{pair}} = 1$, $\pi_{\text{EPC}} = 0$ and $r_{\text{cop}} = 1$. Alternative males (sneakers) (dotted line): $\pi_{\text{pair}} = 0.01$, $\pi_{\text{EPC}} = 2$ and $r_{\text{cop}} = 1$.

This might arise because of differences between populations in the amount of cover available to sneakers at breeding sites (Gross 1991). As a result, territorial males differ in paternity and γ_m , but γ_m is proportional to paternity. It follows that p can be cancelled out and so care is constant. Sneakers differ in both paternity and γ_m but in general p will not cancel out and so there can be a correlation between the paternity of sneakers and their care.

- (ii) *Proportion of sneakers.* Figure 6 illustrates a case in which the proportion of males that are sneakers varies across populations. As the proportion of sneakers increases, the paternity of all males decreases. Although the territorial males find it easier to obtain mates when they are in the minority, this does not make up for their reduced paternity, and effort decreases as the proportion of alternative males increases. As the proportion of alternative males increases, the total number of EPFs increases but the share of EPFs that each of these males gets decreases. As a result, on the rare occasions that they care, their effort is higher.

In the above example, we have varied the proportion of sneakers in the population. Whether it is valid to take this proportion as an input variable depends on what has caused this variation. If the cause does not, in itself, influence any of the factors that determine the relationship between effort and paternity then this approach is reasonable. If, however, the change had been a result of the population changing adaptively to a change in π_{EPC} then our analysis, which assumed π_{EPC} to be constant across populations, would not have been reasonable. The message for empiricists is that in order to make predictions across populations, it is necessary to know what has changed to make populations differ.

9. ISSUE 5: CORRELATIONS ACROSS SPECIES

Møller & Birkhead (1993) and Schwagmeyer *et al.* (1999) use data from birds to analyse the relationship between paternity and male effort across species. Although

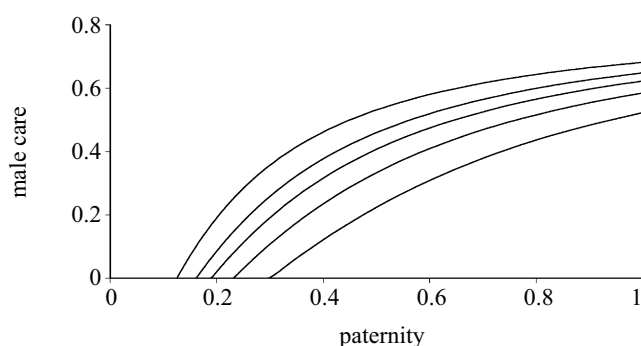


Figure 7. The relationship between paternity and male effort when species differ in the willingness of females to give EPCs. Rate maximization model with $s = 1$, $\lambda = 2$, $\pi_{\text{pair}} = 1$ and $r_{\text{cop}} = 1$. Each curve is generated by varying π_{EPC} . Each curve has a different value of T . From top to bottom, $T = 3.0, 2.0, 1.5, 1.0$ and 0.5 .

these authors discuss their work in the context of theoretical predictions, it is not clear whether these predictions are relevant to the comparative analysis. Predictions are based on the implicit assumption that species differ only in paternity. But why should paternity differ? Paternity is an outcome of the interactions between males and females. If paternity differs between species then these interactions must differ. It follows that paternity cannot vary while everything else is kept constant.

One way in which species could differ is in the willingness of females to give EPCs. As this willingness increases, males will have a lower paternity in their own brood and will find it easier to father offspring in other broods. Both effects will select for a decrease in male parental effort. The resulting relationship between paternity and male effort is illustrated in figure 7. Each curve is generated by varying π_{EPC} while holding the pre-care time, T , constant. Along these curves effort increases with paternity, i.e. the correlation is positive. We note that as p tends to unity effort flattens out and there is a critical p below which effort is zero (cf. Houston 1995).

Werren *et al.* (1980) discuss populations that differ in terms of the ease with which males can obtain EPCs. A male can increase his chances of obtaining EPCs by reducing his care. Werren *et al.* argue that although these populations differ in paternity, paternity may not be the variable that drives effort. Instead, males are reducing their effort in order to gain EPCs as these become easier to obtain. This argument does not seem to hold in our rate maximization model. A general effect that works against the argument of Werren *et al.* is that, as the ease of obtaining EPCs increases, more males will attempt to obtain EPCs and so a male's chance of obtaining EPFs will not increase as rapidly as the increase in EPCs. The argument of Werren *et al.* will apply in some contexts but not in others. Consider the rate maximization model with sex ratio $s = 1$ and all males the same. Males are maximizing $pB - \gamma_m \tau_m$. As the ease with which EPCs are obtained (π_{EPC}) increases, p will decrease drastically. Males will put in less effort and this will decrease γ_f . Since γ_m is constrained to equal γ_f , γ_m will also decrease. Thus in this example the future gain rate decreases as the ease with which EPCs are obtained increases. In other words, the

reduced effort of males is solely the result of their reduced paternity. In the rate maximization model, males are deserting both to gain EPCs and to care for future offspring. Suppose instead that breeding is seasonal and near the end of the season it is too late to pair with a female and raise a brood. The only benefit of desertion may now be the chance to gain EPFs with females in existing pairs. Under these circumstances, the ease with which EPCs can be obtained may well be the most important factor affecting the effort that a male devotes to his current brood.

Figure 7 illustrates the problem of relating paternity and effort across species. The figure shows the paternity and male effort that result when π_{EPC} and the pre-care time, T , are varied. Along each curve, T is constant and effort increases with paternity. Although not shown in the figure, it is also true that effort increases with paternity if T is varied while holding π_{EPC} constant. Thus if species differ only in one of these parameters then a positive correlation between effort and paternity would hold across species. If, instead, species with high T have high π_{EPC} , then a negative correlation could result.

10. DISCUSSION

Many of the results that we present have been illustrated using a model based on rate maximization. Although this approach is obviously an oversimplification, many of the conclusions will be general. Males defend their paternity in various ways, including guarding a female or copulating frequently with her (Birkhead & Møller 1992; Parker 1998). Our rate maximization model is based on the defence of paternity by copulation. We would expect effects similar to those obtained if we had modelled defence by mate guarding. In our model the only decision is the time that is devoted to care. A more detailed approach would consider various other decisions, including the allocation of resources to copulation. This would require a game-theoretical approach, see for example, Parker (1998).

A key feature of our approach is the requirement of consistency. One consistency condition is that the total reproductive success of all males must equal that of all females (Fisher 1930). Queller (1997) realized that this has implications for the relative parental effort of males and females. Our rate maximization model reiterates Queller's conclusions in a simple way. We have also gone beyond Queller's analysis in considering average effort when males differ in ability. A consistent model must account for all of the paternity in a population. Conservation of paternity is explicit in the models of Werren *et al.* (1980) and Gross & Sargent (1985). Both their models and ours show that the way in which paternity is allocated within a population can influence the conclusions that are obtained.

Although it is widely acknowledged that paternity emerges from the interaction between males and females, this fact has largely been ignored in formal models. (For the importance of interactions in the context of mating systems see Alonzo & Warner 2000.) Regarding paternity as an input that can be given any value may produce misleading conclusions. Paternity emerges in a self consistent way from the behaviour of all population members in the models analysed by Hawkes *et al.* (1995) and Kokko (1999). In a consistent model, paternity can only be changed by changing

some other feature of a population. The conclusions that are reached may then depend on the feature that is varied. Thus, for example, assume that we are concerned with data from species that differ in terms of paternity and parental behaviour. Without further information, it is not possible to make a prediction about the relationship between paternity and parental behaviour. If, however, what causes the species to differ in paternity and parental behaviour is known, then a prediction can be made.

When paternity is an outcome, it may be that only some values of paternity may be possible. This is illustrated by the models of Harada & Iwasa (1996), Houston *et al.* (1997) and Iwasa & Harada (1998). In these models the female can control the paternity that a male achieves. In addition to restricting outcomes, allowing paternity to emerge may mean that there are multiple possible solutions to a model, i.e. for given parameters there may be more than one consistent allocation of paternity (cf. McNamara 1994; Heino *et al.* 1997).

In our rate maximization model we can represent a preference by the female for pairing with certain types of males and giving EPCs differentially to different types of males. These preferences are inputs to the model and no attempt has been made to account for the preferences in adaptive terms. If the advantage of copulating with a particular male is based solely on the male's subsequent parental effort, then it is easy to build a consistent model of female behaviour (see Harada & Iwasa 1996; Houston *et al.* 1997; Iwasa & Harada 1998). If the advantage to the female of copulating is not based on the male's efforts, then models sometimes assume a benefit without explicitly incorporating its consequences (Kokko 1999; Alonzo & Warner 2000).

Kempnaers & Sheldon (1997) give a verbal argument for why differences in male ability may result in a negative correlation between effort and paternity. Our approach emphasizes the need to specify the frequency of male types in the population and how these types differ in abilities. Our results provide a rigorous justification of the argument of Kempnaers & Sheldon. They also serve to emphasize that without knowledge of male abilities, it is difficult to make predictions about the correlation between effort and paternity within a population.

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APPENDIX A: REPRODUCTIVE SUCCESS OF THE BROOD IN THE RATE MAXIMIZATION MODEL

Denote the care time of the female by τ_f and the care time of the male by τ_m . We constrain these care times to satisfy

$$\tau_f + \beta\tau_m < 1 \quad (\text{A } 1)$$

and

$$\tau_m + \beta\tau_f < 1, \quad (\text{A } 2)$$

where the parameter β lies in the range $0 \leq \beta < 1$. For τ_f and τ_m in this range, the success of the brood is

$$B(\tau_f, \tau_m) = 4(\tau_f + \tau_m) - 2(\tau_f^2 + \tau_m^2) - 4\beta\tau_f\tau_m \quad (\text{A } 3)$$

For this form of B , the resulting evolutionarily stable care

times always satisfy the above constraints. The interaction parameter β controls how the best care time of one parent depends on the care time of the other. When $\beta = 0$ the best care time of a parent is independent of its partner's care time. The strength of dependence increases as β increases. When $\beta = 1$ there is complete compensation and the model is degenerate in that only one of the parents will devote time to caring. Unless otherwise stated, figures are based on $\beta = 0.2$.

APPENDIX B: AVERAGING OVER CARE TIMES IN THE RATE MAXIMIZATION MODEL

Let $\tau_f(i)$ and $\tau_m(i)$ be the care times of the male and female members of a pair when the male is type i . Let $\gamma_m(i)$ and $p(i)$ be the gain rate and paternity of a male of type i . We assume that success of the brood is as given in Appendix A. Then by criteria (4.1) and (4.3) we have

$$4(1 - \tau_f(i) - \beta\tau_m(i)) = \gamma_f \quad (\text{B } 1)$$

and

$$4(1 - \tau_m(i) - \beta\tau_f(i)) = \gamma_m(i)/p(i). \quad (\text{B } 2)$$

Let $\bar{\tau}_f$ and $\bar{\tau}_m$ be averages over males, as given by equation (5.7). Then multiplying both sides of the above equations by $p(i)$, summing over i and subtracting one equation from the other we have

$$4(1 - \beta)(\bar{\tau}_f - \bar{\tau}_m) = \sum_i p(i) \frac{\gamma_m(i)}{p(i)} - \gamma_f. \quad (\text{B } 3)$$

By equations (5.5) and (5.6)

$$\sum_i p(i) \gamma_m(i) = \gamma_f. \quad (\text{B } 4)$$

Thus we see that if all males have full paternity, then $\bar{\tau}_f = \bar{\tau}_m$, whereas if some males have paternity less than unity then $\bar{\tau}_f > \bar{\tau}_m$.

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